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Research Article

Morpho-phylogenetic evidence reveals novel species and new records of *Nigrograna* (Nigrograna ceae) associated with medicinal plants in Southwestern China

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Abstract

During a survey of saprobic fungal niches in Southwestern China, eighteen ascomycetous collections of *Nigrograna* (Nigrograna ceae, Pleosporales, Dothideomycetes) were found on dead branches of medicinal plants. These taxa were characterized and identified based on morphological and culture characteristics, and phylogenetic analyses of a combined the internal transcribed spacer region of rDNA (ITS), nuclear large subunit rDNA (28S, LSU), RNA polymerase second-largest subunit (*rpb2*), nuclear small subunit rDNA (18S, SSU), and translation elongation factor 1-alpha (*tef1-α*) sequence dataset also confirmed their placement. As a result, four novel species, namely *Nigrograna camelliae*, *N. guttulata*, *N. longiorostiolata* and *N. neriicola* were described. Additionally, four new host records of *N. acericola*, *N. magnoliae*, *N. oleae* and *N. thymi* were introduced. Furthermore, this study addresses the taxonomic status of *N. trachycarpi*, proposing its synonymy under *N. oleae*. Detailed illustrations, descriptions and informative notes for each newly identified taxon and novel host record are provided in this study.

Key words: 4 new taxa, Dothideomycetes, multi-locus, phylogeny, sexual morph, taxonomy

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Introduction

The utilization of medicinal plants is integral to disease prevention and treatment in human life (Nalawade et al. 2003; Cole et al. 2007; Schmidt 2017; Rahman et al. 2019). These plants harbor diverse biological compounds that hold potential for drug development due to their rich reservoir of bioactive ingredients (Samy and Gopalakrishnakone 2007; Ali et al. 2021; Atanasov et al. 2021). Southwestern China, recognized as one of the primary regions for traditional Chinese herbal medicine, boasts remarkable diversity in medicinal plant species. This diversity is largely driven by the region's unique karst landforms, which

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promote species differentiation and abundance (Huang et al. 2012; Taylor et al. 2014; Lu et al. 2018; Guo et al. 2020; Shan et al. 2022). Recent studies in Southwest China have revealed novel micro-fungi species associated with medicinal plants, including pathogens (Abtahi and Nourani 2017), saprobes (Du et al. 2022a; Sun et al. 2023; Wu et al. 2024) and endophytes (Helaly et al. 2018; Keshri et al. 2021; Du et al. 2022b), highlighting the potential of these plants as reservoirs for discovering fungal diversity.

Nigrogranaceae (Pleosporales, Dothideomycetes) was established by Jaklitsch and Voglmayr (2016) based on morpho-molecular evidence, with *Nigrograna* as the type genus. The divergence of Nigrogranaceae is established at approximately 79 (44–124) Mya in crown age and 131 (86–180) Mya in stem age (Liu et al. 2017). Initially, the genus *Nigrograna* was proposed by de Gruyter et al. (2012) to accommodate *Pyrenochaeta mackinnonii* (a pathogenic species in humans isolated from a mycetoma patient), which was later synonymized as *Nigrograna mackinnonii*. However, phylogenetic studies revealed that *N. mackinnon*ii was closely related to *Biatriospora marina*, the type species of the monotypic genus *Biatriospora* (Ahmed et al. 2014), leading to the reclassification of *N. mackinnonii* as *Biatriospora mackinnonii* (Ahmed et al. 2014). Jaklitsch and Voglmayr (2016) subsequently proposed the family Nigrograna-ceae, describing three new taxa that differed significantly from *Biatriospora* in morphology and ecology. Hongsanan et al. (2020) further revised the taxonomic status of *Biatriospora* and *Nigrograna*, suggesting that both genera should be retained. To date, there are 37 species epithets of *Nigrograna* listed in Index Fungorum (http://www.indexfungorum.org/Names/Names.asp; accessed 7 September 2024).

Most members of *Nigrograna* have cryptic morphological characters, leading Jaklitsch and Voglmayr (2016) to classify them as cryptic species. The sexual morphs of *Nigrograna* are characterized by having globose to subglobose ascomata with ostiole, multi-layered peridium, clavate and fissitunicate asci, fusoid to narrowly ellipsoid, straight or curved, septate, and smooth or verruculose ascospores (Jaklitsch and Voglmayr 2016; Zhang et al. 2020; Lu et al. 2022). In contrast, the asexual morphs are defined by globose to subglobose or pyriform pycnidia, filiform and branched conidiophores, hyaline, phialidic and discrete conidiogenous cells, sub-hyaline, aseptate and ellipsoidal conidia (de Gruyter et al. 2012; Jaklitsch and Voglmayr 2016; Lu et al. 2022). The life modes of *Nigrograna* species are diverse, ranging from endophytic and saprobic to pathogenic (in human) (Kolařík 2018; Zhao et al. 2018; Lu et al. 2022; Li et al. 2023). These species have been reported from various hosts in terrestrial, marine, and freshwater habitats (Hyde et al. 2017; Tibpromma et al. 2017; Dayarathne et al. 2020; Lu et al. 2022; Bundhun et al. 2023; Hu et al. 2023; Li et al. 2023; Senanayake et al. 2023; Shu et al. 2023), underscoring the broad ecological diversity of this genus. In recent years, an increasing number of new species and records of *Nigrograna* have been reported from various hosts in China. Most of these species have been identified as saprotrophic fungi from terrestrial habitats (Tibpromma et al. 2017; Boonmee et al. 2021; de Silva et al. 2022; Lu et al. 2022; Hu et al. 2023; Li et al. 2023; Liu et al. 2024; Ren et al. 2024; Xu et al. 2024). However, reports of *Nigrograna* occurring on medicinal plants are

limited. Given the ecological and economic importance of these plants, it is essential to explore the taxonomy and phylogeny of *Nigrograna* species associated with medicinal flora. Such investigations will deepen our understanding of fungal diversity in these specialized niches and may reveal new insights into the potential applications of these fungi.

This study focuses on elucidating the diversity of Nigrogranaceae in Southwestern China, identifying eight species associated with medicinal plants. We aim to describe these novel findings and contribute to the understanding of fungal diversity in this region. Through a combination of morphological comparisons and multi-locus phylogenetic analyses, we introduce four new species and four new host records, supported by both morphological and phylogenetic evidence.

Materials and methods

Collection and examination of specimens

Specimens in this study were collected from medicinal plants of nine families (Apocynaceae, Berberidaceae, Buxaceae, Celastraceae, Eucommiaceae, Fabaceae, Primulaceae, Rutaceae and Theaceae) in Southwest China during 2021 and 2023, viz., (1) Guizhou Province (26°30'43"N–26°32'18"N, 106°39'32"E–106°41'48"E, elevation 1,127–1,155 m); (2) Sichuan Province (29°29'1"N–31°8'4"N, 103°2'23"E–104°14'19"E, elevation 504–1,200 m); (3) Yunnan Province (21°55'53"N–25°14'27"N, 101°23'19"E–102°44'28"E, elevation 505–1,922 m). The sampling information (date, host, place, GPS, etc.) was recorded. Samples were packaged in envelopes and brought to the laboratory following the method described by Senanayake et al. (2020). Morphological observations were made using a Motic SMZ (Stereoscopic Zoom Microscope) 168 Series dissecting microscope (Motic, Xiamen, China) for fungal structures on a natural substrate. Fruiting bodies were collected using a syringe needle and transferred to a drop of tap water on a clean slide. The features were examined and photographed using a Nikon ECLIPSE Ni-U compound microscope fitted with a Nikon DS-Ri2 digital camera. Measurements were made with the Tarosoft Image Frame Work v. 0.9.7 software following the procedures outlined by Liu et al. (2010), and images used for photo plates were processed with Adobe Photoshop CC 2018 software (Adobe Systems, San Jose, CA, USA). Single spore isolations were made on potato dextrose agar (PDA, Oxoid) or water agar (WA, Oxoid) and later transferred onto new PDA plates following the methods described in Senanayake et al. (2020). Incubation and cultural growth were observed at 25 °C in dark and pure cultures were obtained.

Herbarium specimens were deposited in the Herbarium of Cryptogams, Kunming Institute of Botany Academia Sinica (HKAS), Kunming, China, and the herbarium of University of Electronic Science and Technology (HUEST), Chengdu, China. The pure cultures obtained in this study were deposited in the China General Microbiological Culture Collection Center (CGMCC) in Beijing, China and the University of Electronic Science and Technology Culture Collection (UESTCC), Chengdu, China. Names of the new taxa were registered in MycoBank (http://www.mycobank.org/).

DNA extraction, PCR amplification and sequencing

Isolates were grown in PDA medium at 25 °C in dark for three weeks to one month. Fungal mycelia were scraped off and transferred to 1.5 mL microcentrifuge tubes using a sterilized lancet for genomic DNA extraction. Fungal DNA was extracted from mycelia (about 50–100 mg) using the Trelief TM Plant Genomic DNA Kit (TsingKe Co., Beijing, China). Five different gene regions were amplified by Polymerase Chain Reaction (PCR). The internal transcribed spacer region of rDNA (ITS), nuclear large subunit rDNA (28S, LSU), nuclear small subunit rDNA (18S, SSU), RNA polymerase second-largest subunit (*rpb2*) and translation elongation factor 1-alpha (*tef1-α*) were selected for the study. The primers used were LR0R/LR5 for LSU (Vilgalys and Hester 1990), NS1/NS4 for SSU (White et al. 1990), ITS5/ITS4 for ITS (White et al. 1990), fRPB2-5F and fRPB2-7cR for *rpb2* (Liu et al. 1999) and TEF1-983F/TEF1-2218R for *tef1-α* (Rehner and Buckley 2005). Amplifications were performed in a 25 µL reaction volume containing 9.5 µL of ddH_2O, 12.5 µL of 2× Taq PCR Master Mix with blue dye (Sangon Biotech, Shanghai, China), 1 µL of DNA template and 1 µL of each primer. The amplification condition for ITS, LSU, SSU, and *tef1-α* consisted of initial denaturation at 94 °C for 3 min, followed by 40 cycles of 45 s at 94 °C, 50 s at 55 °C and 1 min at 72 °C, and a final extension period of 10 min at 72 °C. The amplification condition for the *rpb2* gene consisted of initial denaturation at 95 °C for 5 min; followed by 37 cycles of 15 s at 95 °C, 50 s at 56 °C and 2 min at 72 °C, and a final extension period of 10 min at 72 °C. The PCR product purification and sequencing were performed at Beijing Tsingke Biotechnology (Chengdu) Co., Ltd., Chengdu, China.

Phylogenetic analyses

In this study, the taxa included in the phylogenetic analyses were selected and obtained from previous studies and GenBank (Table 1), with a total of 67 taxa. *Occultibambusa pustula* (MFLUCC 11-0502) and *O. bambusae* (MFLUCC 13-0855) (Occultibambusaceae, Pleosporales) were selected as outgroup taxa. Single-locus alignments were made in MAFFT v. 7 (http://mafft.cbrc.jp/alignment/server/) (Katoh and Standley 2013) and checked visually using AliView (Larsson 2014). The alignments were trimmed using trimAl v 1.2 (Capella-Gutierrez et al. 2009). Five single-locus alignments were combined using SequenceMatrix 1.7.8 (Vaidya et al. 2011). Maximum likelihood (ML) and Bayesian inference (BI) analyses were employed to assess phylogenetic relationships as detailed in Dissanayake et al. (2020).

ML analyses were performed with RAxML-HPC v.8 on XSEDE (8.2.12) (Stamatakis 2006; Stamatakis et al. 2008) through the CIPRES Science Gateway V. 3.3 (https://www.phylo.org/portal2/login!input.action) (Miller et al. 2010). The tree search included 1,000 non-parametric bootstrap replicates; the best scoring tree was selected among suboptimal trees from each run by comparing likelihood scores under the GTRGAMMA substitution model. The resulting replicates were plotted onto the best scoring tree obtained previously. ML bootstrap values equal to or greater than 75% were marked near each node.

BI was performed in MrBayes 3.2.6 (Ronquist et al. 2012). The program MrModeltest 2 v. 2.3 (Nylander 2008) was used to determine the best nucleotide

substitution model for each data partition. The evolutionary model of SYM+I+G substitution model was selected for ITS, HKY+G substitution model was selected for SSU, and GTR+I+G substitution model was selected for LSU, *rpb2* and *tef1-α*. Posterior probabilities (PP) (Rannala and Yang 1996) were determined by Markov chain Monte Carlo sampling (MCMC). Six simultaneous Markov chains were run for 10 million generations, and trees were sampled every 1,000 th generation. The first 25% of saved trees, representing the burn-in phase of the analysis, were discarded. The remaining trees were used for calculating posterior probabilities in the majority rule consensus tree (Larget and Simon 1999). PP values equal to or greater than 0.95 were marked near each node.

Phylogenetic trees were printed with Fig Tree v. 1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/) and the layout was created in Adobe Illustrator CS6 software (Adobe Systems, USA). The new sequences generated in this study were deposited in GenBank (Table 1).

Table 1. Taxa used in the phylogenetic analyses and the corresponding GenBank accession numbers.

Taxa names	Strain/Specimen number	GenBank accession numbers					References
		ITS	LSU	*rpb2*	SSU	*tef1-α*	
Nigrograna acericola	CGMCC 3.24957 T	OR253153	OR253312	N/A	N/A	OR263572	Li et al. (2023)
Nigrograna acericola	**UESTCC 23.0208**	**PP812425**	**PP812460**	**PP838917**	**PP812443**	**PP838935**	**In this study**
Nigrograna acericola	**UESTCC 23.0191**	**PP812426**	**PP812461**	**PP838918**	**PP812444**	**PP838936**	**In this study**
Nigrograna antibiotica	CCF 4378 T	JX570932	KF925327	N/A	KF925328	JX570934	Kolařík (2018)
Nigrograna antibiotica	CCF 4498	LT221894	LT221895	N/A	N/A	N/A	Kolařík (2018)
Nigrograna aquatica	MFLUCC 17-2318 T	MT627705	MN913705	N/A	N/A	N/A	Dong et al. (2020)
Nigrograna asexualis	ZHKUCC 22-0214 T	OP450965	OP450971	OP432241	OP450979	OP432245	Lu et al. (2022)
Nigrograna camelliae	**CGMCC 3.25625 T**	**PP812431**	**PP812466**	**PP838923**	**PP812449**	**PP838939**	**In this study**
Nigrograna camelliae	**UESTCC 23.0197**	**PP812432**	**PP812468**	**PP838924**	**PP812450**	**PP838940**	**In this study**
Nigrograna cangshanensis	MFLUCC 15-0253 T	KY511063	KY511064	N/A	KY511065	N/A	Tibpromma et al. (2017)
Nigrograna carollii	CCF 4484 T	LN626657	LN626682	LN626662	LN626674	LN626668	Kolařík (2018)
Nigrograna chromolaenae	MFLUCC 17-1437 T	MT214379	MT214473	N/A	N/A	MT235801	Mapook et al. (2020)
Nigrograna coffeae	ZHKUCC 22-0210 T	OP450967	OP450973	OP432243	OP450981	OP432247	Lu et al. (2022)
Nigrograna coffeae	ZHKUCC 22-0211	OP450968	OP450974	OP432244	OP450982	OP432248	Lu et al. (2022)
Nigrograna fuscidula	CBS 141556 T	KX650550	N/A	N/A	N/A	KX650525	Jaklitsch and Voglmayr (2016)
Nigrograna fuscidula	CBS 141476	KX650547	N/A	KX650576	KX650509	KX650522	Jaklitsch and Voglmayr (2016)
Nigrograna guizhouensis	CGMCC 3.25501 T	OR680498	OR680565	OR842915	OR680867	OR858897	Zhang et al. (2024)
Nigrograna guizhouensis	ZY22.020	OR680499	OR680566	OR842916	OR680868	OR858898	Zhang et al. (2024)
Nigrograna guttulata	**CGMCC 3.25689 T**	**PP812433**	**PP812469**	**PP838925**	**PP812451**	**PP838941**	**In this study**
Nigrograna guttulata	**UESTCC 23.0295**	**PP812434**	**PP812470**	**PP838926**	**PP812452**	**PP838942**	**In this study**
Nigrograna heveae	ZHKUCC 22-0284 T	OP584490	OP584488	OP750374	OP584492	OP750372	Hyde et al. (2023)
Nigrograna hydei	GZCC 19-0050 T	MN387225	MN387227	N/A	N/A	MN389249	Zhang et al. (2020)
Nigrograna impatientis	GZCC 19-0042 T	MN387226	MN387228	N/A	N/A	MN389250	Zhang et al. (2020)
Nigrograna italica	MFLU 23-0139 T	OR538590	OR538591	OR531365	N/A	OR531366	Bundhun et al. (2023)
Nigrograna jinghongensis	KUMUCC 21-0035 T	MZ493303	MZ493317	MZ508421	MZ493289	MZ508412	Boonmee et al. (2021)
Nigrograna jinghongensis	KUMUCC 21-0036	MZ493304	MZ493318	MZ508422	MZ493290	MZ508413	Boonmee et al. (2021)
Nigrograna kunmingensis	ZHKUCC 22-0242 T	OP456214	OP456379	N/A	OP456382	OP471608	Liu et al. (2024)
Nigrograna kunmingensis	ZHKUCC 22-0243	OP484334	OP456380	N/A	OP456383	OP471609	Liu et al. (2024)
Nigrograna lincangensis	ZHKUCC 23-0798 T	OR853099	OR922323	OR966280	OR941079	OR966282	Xu et al. (2024)
Nigrograna lincangensis	ZHKUCC 23-0799	OR853100	OR922324	OR966281	OR941080	OR966283	Xu et al. (2024)

Taxa names	Strain/Specimen number	GenBank accession numbers					References
		ITS	LSU	*rpb2*	SSU	*tef1-α*	
Nigrograna locuta-pollinis	CGMCC 3.18784 T	MF939601	MF939583	MF939610	N/A	MF939613	Zhao et al. (2018)
Nigrograna longiorostiolata	**CGMCC 3.25626 T**	**PP812421**	**PP812458**	**PP838913**	**PP812439**	**PP838945**	**In this study**
Nigrograna longiorostiolata	**UESTCC 23.0200**	**PP812422**	**PP812457**	**PP838914**	**PP812440**	**PP838946**	**In this study**
Nigrograna mackinnonii	CBS 674.75 T	KF015654	KF015612	KF015703	GQ387552	KF407986	de Gruyter et al. (2012)
Nigrograna magnoliae	MFLUCC 20-0020 T	MT159628	MT159622	MT159611	MT159634	MT159605	Wanasinghe et al. (2020)
Nigrograna magnoliae	MFLUCC 20-0021	MT159629	MT159623	MT159612	MT159635	MT159606	Wanasinghe et al. (2020)
Nigrograna magnoliae	**UESTCC 23.0203**	**PP812419**	**PP812454**	**PP838929**	**PP812437**	**PP838943**	**In this study**
Nigrograna magnoliae	**CGMCC 3.25627**	**PP812420**	**PP812453**	**PP838927**	**PP812435**	**PP838931**	**In this study**
Nigrograna magnoliae	**UESTCC 23.0190**	**PP812417**	**PP812456**	**PP838930**	**PP812438**	**PP838944**	**In this study**
Nigrograna magnoliae	**UESTCC 23.0206**	**PP812418**	**PP812455**	**PP838928**	**PP812436**	**PP838932**	**In this study**
Nigrograna mycophila	CBS 141478 T	KX650553	N/A	N/A	N/A	KX650526	Jaklitsch and Voglmayr (2016)
Nigrograna mycophila	CBS 141483	KX650555	N/A	KX650577	KX650510	KX650528	Jaklitsch and Voglmayr (2016)
Nigrograna neriicola	**CGMCC 3.25624 T**	**PP812430**	**PP812467**	**PP838921**	**PP812447**	**PP838937**	**In this study**
Nigrograna neriicola	**UESTCC 23.0195**	**PP812429**	**PP812465**	**PP838922**	**PP812448**	**PP838938**	**In this study**
Nigrograna norvegica	CBS 141485 T	KX650556	N/A	KX650578	KX650511	N/A	Jaklitsch and Voglmayr (2016)
Nigrograna obliqua	CBS 141477 T	KX650560	N/A	KX650580	N/A	KX650531	Jaklitsch and Voglmayr (2016)
Nigrograna obliqua	CBS 141475	KX650558	N/A	KX650579	KX650512	KX650530	Jaklitsch and Voglmayr (2016)
Nigrograna oleae	CGMCC 3.24423 T	OR253080	OR253232	N/A	N/A	OR262140	Li et al. (2023)
***Nigrograna oleae* (*N. trachycarpi*)**	**GMB0499**	**OR120437**	**N/A**	**N/A**	**N/A**	**OR150024**	Hu et al. (2023); **In this study**
***Nigrograna oleae* (*N. trachycarpi*)**	**GMB0505**	**OR120440**	**N/A**	**N/A**	**N/A**	**OR150025**	Hu et al. (2023); **In this study**
Nigrograna oleae	**UESTCC 23.0209**	**PP812424**	**PP812463**	**PP838915**	**PP812441**	**PP838933**	**In this study**
Nigrograna oleae	**UESTCC 23.0193**	**PP812423**	**PP812459**	**PP838916**	**PP812442**	**PP838934**	**In this study**
Nigrograna peruviensis	CCF 4485 T	LN626658	LN626683	LN626665	LN626677	LN626671	Kolařík (2018)
Nigrograna puerensis	ZHKUCC 22-0212 T	OP450969	OP450975	N/A	OP450983	OP432249	Lu et al. (2022)
Nigrograna rhizophorae	MFLUCC 18-0397 T	MN047085	N/A	MN431489	N/A	MN077064	Dayarathne et al. (2020)
Nigrograna rubescens	CHEM 2344 T	OQ400924	OQ400934	OQ413082	N/A	OQ413077	Mack et al. (2024)
Nigrograna samueliana	NFCCI 4383 T	MK358817	MK358812	MK330939	MK358810	MK330937	Dayarathne et al. (2020)
Nigrograna schinifolii	GMB0498 T	OR120434	N/A	N/A	N/A	OR150022	Hu et al. (2023)
Nigrograna schinifolii	GMB0504	OR120441	N/A	N/A	N/A	OR150023	Hu et al. (2023)
Nigrograna sichuanensis	CGMCC 3.24424 T	OR253096	OR253248	N/A	N/A	OR251058	Li et al. (2023)
Nigrograna thailandica	MFLUCC 17-2663	MK762709	MK762716	N/A	MK762704	N/A	Senanayake et al. (2023)
Nigrograna thymi	MFLUCC 14-1096 T	KY775576	KY775573	N/A	KY775574	KY775578	Hyde et al. (2017)
Nigrograna thymi	**UESTCC 23.0210**	**PP812428**	**PP812464**	**PP838919**	**PP812445**	**N/A**	**In this study**
Nigrograna thymi	**UESTCC 23.0194**	**PP812427**	**PP812462**	**PP838920**	**PP812446**	**N/A**	**In this study**
Nigrograna verniciae	CGMCC 3.24425	OR253116	OR253275	N/A	N/A	OR251168	Li et al. (2023)
Nigrograna wuhanensis	ZHKUCC 22-0329 T	OP941389	OP941390	N/A	OQ061465	OP947079	Shu et al. (2023)
Nigrograna yasuniana	YU 101026 T	HQ108005	LN626684	LN626664	LN626676	LN626670	Kolařík (2018)
Occultibambusa bambusae	MFLUCC 13-0855 T	KU940123	KU863112	KU940170	N/A	KU940193	Dai et al. (2017)
Occultibambusa pustula	MFLUCC 11-0502 T	KU940126	KU863115	N/A	N/A	N/A	Dai et al. (2017)

*** Remarks:** The superscript T denotes ex-type isolates. "N/A" denotes sequence is unavailable. The newly generated sequences, new species and synonymized isolates are indicated in black bold font. **Abbreviations: CBS:** CBS–KNAW Fungal Biodiversity Centre, Utrecht, The Netherlands; **CCF:** Culture Collection of Fungi, Charles University, Prague, Czech Republic; **CGMCC:** China General Microbiological Culture Collection Center, Institute of Microbiology, Chinese Academy of Sciences, Beijing, China; **GMB:** Herbaria of Guizhou Medical University, Guiyang, China; **GZCC:** Guizhou Culture Collection, Guizhou, China; **KUMUCC:** Kunming Medical University Culture Collection, Kunming, China; **MFLUCC:** Mae Fah Luang University Culture Collection, Chiang Rai, Thailand; **NFCCI:** National Fungal Culture Collection of India, India; **UESTCC:** University of Electronic Science and Technology Culture Collection, Chengdu, China; **YU:** Yale University Herbarium, Connecticut, America; **ZHKUCC:** Zhongkai University of Agriculture and Engineering Culture Collection, Guangzhou, China; **Personal collections**: **ZY** and **CHEM:** These numbers are assigned by the author and have no annotations.

Phylogenetic results

In this study, five loci, ITS, LSU, *rpb2*, SSU, and *tef1-α*, were used to determine the phylogenetic placement of the new collections. The concatenated matrix was comprised of 69 taxa with a total of 4,236 bp characters (ITS: 1–473 bp; LSU: 474–1,306 bp; *rpb2*: 1,307–2,331 bp; SSU: 2,332–3,335 bp; *tef1-α*: 3,336–4,236 bp) including gaps. Single-locus analyses were carried out to compare the topologies and clade stabilities, respectively. The results showed that ML and BI were similar in topology without significant conflicts. The best RAxML tree with a final likelihood value of -20,464.246121 is presented in Fig. 1. RAxML analysis yielded 1,200 distinct alignment patterns and 26.42% of undetermined characters or gaps. Estimated base frequencies were as follows: A = 0.247595, C = 0.247214, G = 0.264771, T = 0.240420, with substitution rates AC = 1.651782, AG = 5.572876, AT = 1.491922, CG = 1.179397, CT = 11.546850, GT = 1.000000; gamma distribution shape parameter alpha = 0.139617. Tree-Length = 1.453662. The final average standard deviation of split frequencies at the end of total MCMC generations for BI analysis was 0.009978 (the critical value for the topological convergence diagnostic is below 0.01).

Representatives of all the species of *Nigrograna* were including in our phylogenetic analysis (Fig. 1). Four strains (CGMCC 3.25627, UESTCC 23.0203, UESTCC 23.0190 and UESTCC 23.0206) were nested with *N. magnoliae* (ex-type strain MFLUCC 20-0020 and MFLUCC 20-0021), and strains, UESTCC 23.0208 and UESTCC 23.0191, UESTCC 23.0210 and UESTCC 23.0194, clustered with *N. acericola* (ex-type strain, CGMCC 3.24957) and *N. thymi* (ex-type strain, MFLUCC 14-1096), respectively. *Nigrograna trachycarpi* (GMB0499 and GMB0505) was synonymized under *N. oleae*, these two strains of *N. trachycarpi* and our two isolates (UESTCC 23.0209 and UESTCC 23.0193) grouped with ex-type strain of *N. oleae* (CGMCC 3.24423) with maximum support (100% MLBS/1.00 BIPP).

Nigrograna camelliae (CGMCC 3.25625 and UESTCC 23.0197) and *N. guttulata* (CGMCC 3.25689 and UESTCC 23.0295) were sister to *N. coffeae* (ex-type strain ZHKUCC 22-0210 and ZHKUCC 22-0211) and *N. peruviensis* (ex-type strain CCF 4485), respectively. They formed two distinct clades with 100% MLBS/1.00 BIPP and 63% MLBS/0.98 BIPP, respectively. *Nigrograna neriicola* (CGMCC 3.25624 and UESTCC 23.0195) was sister to *N. schinifolii* (ex-type strain GMB0498 and GMB0504) and formed a strongly supported monophyletic lineage (96% MLBS/1.00 BIPP). *Nigrograna longiorostiolata* (CGMCC 3.25626 and UESTCC 23.0200) formed a distinct lineage with high bootstrap support (100% MLBS/1.00 BIPP).

Taxonomy

***Nigrograna magnoliae* Wanas, PLoS One, 15(7): 10 (2020)**

MycoBank No: 557331

Fig. 2

Description. ***Saprobic*** on dead branches of *Buxus sinica* (Buxaceae). **Sexual morph:** ***Ascomata*** 204–326 µm wide, 140–220 µm high ($\bar{x}$ = 248 × 187 µm, n = 20), solitary or gregarious, scattered, immersed to semi-immersed, with only ostiolar necks visible on the host surface, trigonoid, uniloculate, perithecioid, globose to subglobose, brown to dark brown, with an ostiole. ***Ostiole*** central or eccentric,

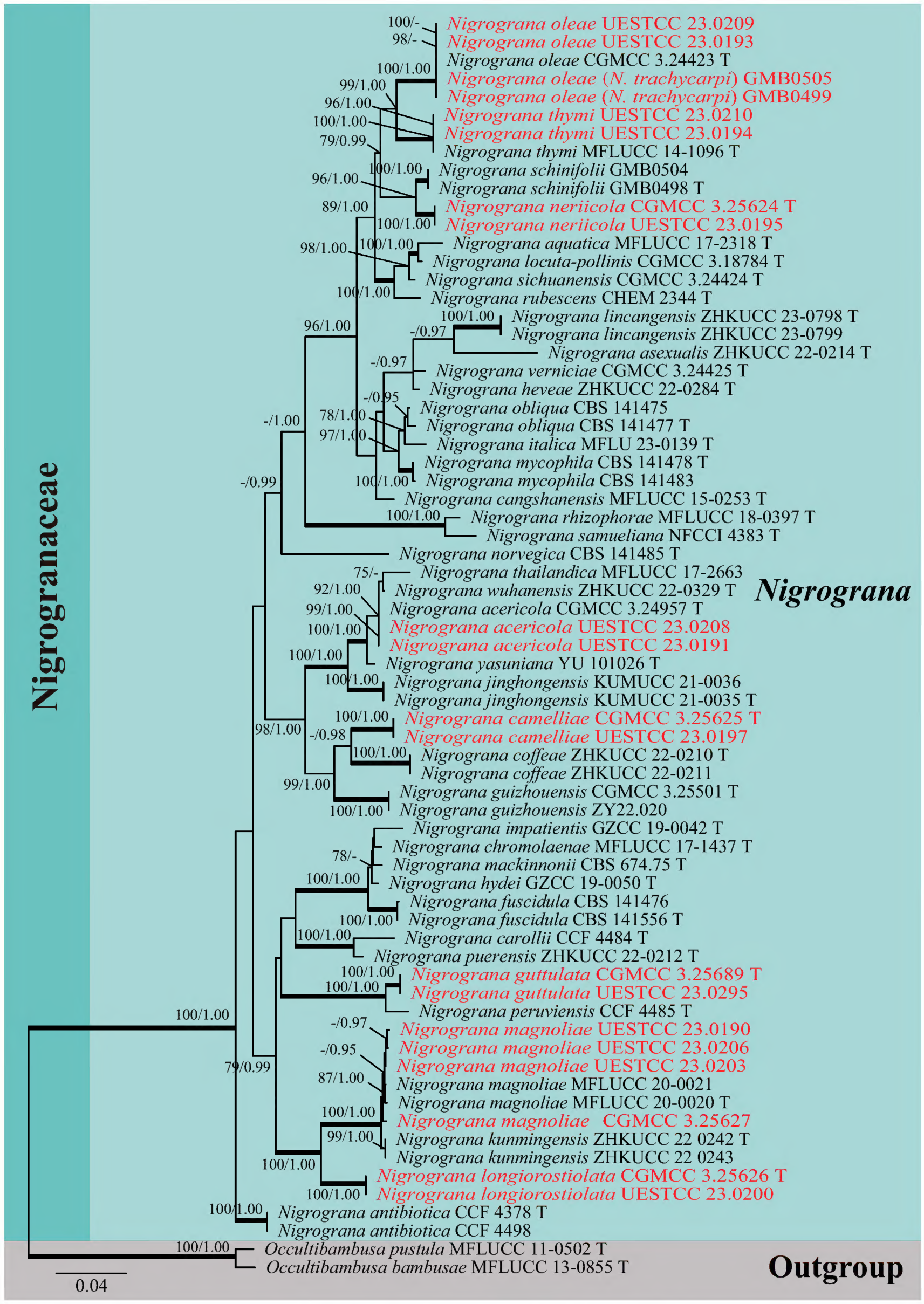

Figure 1. Phylogenetic tree constructed from maximum likelihood (RAxML) analyses of a combined ITS, LSU, *rpb2*, SSU, and *tef1-α* sequence data for selected genera within the family Nigrograna (Pleosporales, Dothideomycetes). Branches support for Maximum likelihood (MLBS) equal to or greater than 75% and Bayesian inference posterior probabilities (BIPP) equal to or greater than 0.95 are marked above or below nodes as MLBS/BIPP. The abbreviation T indicates the ex-type strain. Species names and culture collections in red are newly collected taxa and synonymized isolates. The tree was rooted with *Occultibambusa pustula* (MFLUCC 11-0502) and *O. bambusae* (MFLUCC 13-0855).

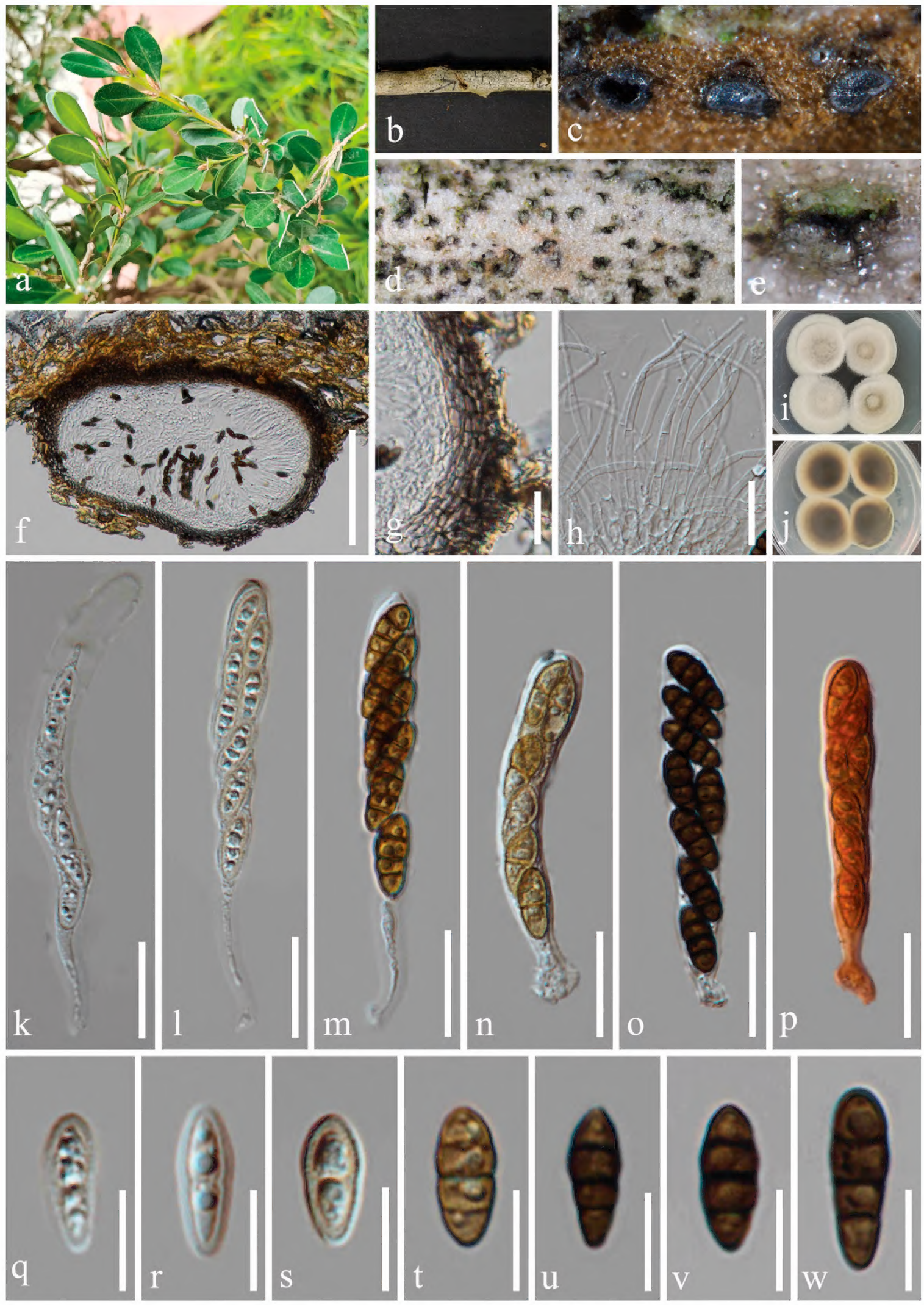

Figure 2. *Nigrograna magnoliae* (HUEST 23.0203, new host record) **a** host *Buxus sinica* **b** branch of *Buxus sinica* **c–e** appearance of ascomata on host surface **f** vertical section through ascoma **g** peridium **h** hamathecium **i, j** colonies on PDA, above (**i**) and below (**j**) **k–o** asci **p** asci in Congo red **q–w** ascospores. Scale bars: 100 μm (**f**); 20 μm (**g, h, k–p**); 10 μm (**q–w**).

brittle. ***Peridium*** 15–23 μm ($\bar{x}$ = 18 μm, n = 20) composed of angular cells, consisting 4–5 layers, brown to dark brown thick-walled cells of outer layer, hyaline to subhyaline thin-walled cells of inner layer. ***Hamathecium*** 1–3 μm ($\bar{x}$ = 2 μm, n = 20) wide, composed of numerous, filamentous, hyaline, aseptate or separate, rarely branched, smooth-walled pseudoparaphyses. ***Asci*** 57–103 × 8–11 μm ($\bar{x}$ = 72.5 × 10 μm, n = 30), 8-spored, bitunicate, fissitunicate, clavate to long cylindric-clavate, short cylindrical pedicellate with a swollen base, apically rounded, with a minute

ocular chamber. ***Ascospores*** 13–19 × 4.5–6 µm ($\bar{x}$ = 14.5 × 5 µm, n = 50), 1–2-seriate, partially overlapping, fusoid to ellipsoid, tapering towards the blunt ends, or blunt at both ends, guttulate, smooth-walled, olivaceous to yellowish-brown when young, 1-septate; deeply constricted at septa, becoming 3-septate, brown to dark brown when mature, without appendages. **Asexual morph:** Undetermined.

Culture characteristics. Ascospores germinated on PDA within 24 h, and germ tubes produced from basal cell. Colonies growing on PDA reached 32–33 mm in diameter after three weeks at 25 °C in dark, white in the whole colony from above, and slightly raised in the center, circular, flat, edge entire, margin well-defined; in reverse, grayish black in the center, off-white at the margin, the color gradually lightens from center to edge, no pigmentation on PDA.

Material examined. CHINA • Yunnan Province, Kunming City, Panlong District, Kunming Botanical Garden. 25°8'27"N, 102°44'24"E, elevation 1,922 m, on dead branches of medicinal plant *Buxus sinica* (Rehder & E. H. Wilson) M. Cheng (Buxaceae), 11 November 2022, H.Z. Du, S735 (HUEST 23.0203), living culture UESTCC 23.0203; • ibid., Sichuan Province, Chengdu City, High-tech West District, Yaobo Park, 30°43'57"N, 103°56'21"E, elevation 504 m, on dead branches of medicinal plant *Eucommia ulmoides* Oliv. (Eucommiaceae), 11 August 2021, H.Z. Du, S347 (HUEST 23.0206), living culture UESTCC 23.0206; • ibid., Guizhou Province, Guiyang City, Nanming District, Guiyang Medicinal Botanical Garden, 26°32'18"N, 106°41'48"E, elevation 1,127 m, on dead branches of medicinal plant *Mahonia bealei* (Fort.) Carr. (Berberidaceae), 12 October 2021, H.Z. Du, S370 (HUEST 23.0207), living culture CGMCC 3.25627 = UESTCC 23.0207; • ibid., Guizhou Province, Guiyang City, Huaxi District, 26°30'43"N, 106°39'32"E, elevation 1,155 m, on dead branches of medicinal plant *Camellia sinensis* (L.) O. Ktze. (Theaceae), 2 February 2023, Y.X. Yu, GY33 (HUEST 23.0190), living culture UESTCC 23.0190.

Notes. *Nigrograna magnoliae* was introduced by Wanasinghe et al. (2020) with both asexual and sexual morphs reported in China. The host distribution of this species is presented in Table 2. Our collections are identical to *N. magnoliae* based on morphology and phylogeny. Therefore, we reported it as new host records from medicinal plants of *Buxus sinica*, *Camellia sinensis*, *Eucommia ulmoides* and *Mahonia bealei* in China.

Table 2. The host distribution of *Nigrograna magnoliae*.

Host distribution	Collecting sites	References
Magnolia denudate (Magnoliaceae)	China (Yunnan Province)	Wanasinghe et al. (2020)
Submerged wood from aquatic habitats	Thailand (Chiang Rai Province)	Zhang et al. (2020)
Decaying twigs of unidentified host	China (Guizhou Province)	Zhang et al. (2020)
Acer truncatum (Aceraceae)	China (Sichuan Province)	Li et al. (2023)
Juglans regia (Juglandaceae)	China (Sichuan Province)	Li et al. (2023)
Olea europaea (Oleaceae)	China (Sichuan Province)	Li et al. (2023)
Michelia alba (Magnoliaceae)	China (Guizhou Province)	Chethana et al. (2023)
Rosa sp. (Rosaceae)	China (Sichuan Province)	Chethana et al. (2023)
Fruiting bodies of *Shearia* sp. (Dothioraceae)	China (Guizhou Province)	Chethana et al. (2023)
Magnolia grandiflora (Magnoliaceae)	Thailand (Chiang Mai Province)	https://www.ncbi.nlm.nih.gov/nuccore/MN081891.1
Castanopsis indica (Fagaceae)	China (Yunnan Province)	Ren et al. (2024)
Buxus sinica (Buxaceae)	China (Yunnan Province)	In this study
Eucommia ulmoides (Eucommiaceae)	China (Sichuan Province)	In this study
Mahonia bealei (Berberidaceae)	China (Guizhou Province)	In this study
Camellia sinensis (Theaceae)	China (Guizhou Province)	In this study

Nigrograna longiorostiolata **H.Z. Du & Jian K. Liu, sp. nov.**
MycoBank No: 854177
Fig. 3

Etymology. The epithet '*longiorostiolata*' refers to the longer-ostiolate of ascomata.

Holotype. HKAS 131311

Description. ***Saprobic*** on dead branches of *Citrus medica* (Rutaceae). **Sexual morph:** ***Ascomata*** 222–293 µm wide, 144–486 µm high ($\bar{x}$ = 264 × 303 µm, n = 20), solitary, scattered, immersed, visible as black dots on the host surface, uniloculate, globose to subglobose, sometimes obpyriform with a long ostiole. ***Ostioles*** 175–302 µm long, 83–128 µm wide ($\bar{x}$ = 263 × 102 µm, n = 20) central or eccentric, longer, with a crest-like apex, filled with hyaline or slightly brown periphyses. ***Peridium*** 17–32 µm ($\bar{x}$ = 23.5 µm, n = 20) composed of *textura prismatica* cells, consisting 3–4 layers, brown to dark brown of outer layer, hyaline to subhyaline of inner layer. ***Hamathecium*** 1–2 µm ($\bar{x}$ = 1.5 µm, n = 20) wide, composed of numerous, filiform, hyaline, aseptate or separate, rarely branched, guttulate, smooth-walled pseudoparaphyses. ***Asci*** 40–70 × 6–9 µm ($\bar{x}$ = 53 × 8 µm, n = 30), 5–8-spored, bitunicate, fissitunicate, clavate, short cylindrical pedicellate with a swollen base, apically rounded, with a minute ocular chamber. ***Ascospores*** 10–13 × 4–6 µm ($\bar{x}$ = 12 × 5 µm, n = 50), 1–2-seriate, partially overlapping, fusoid to ellipsoid, tapering towards the blunt ends, or blunt at both ends, guttulate, olivaceous to yellowish-brown when young, aseptate or 1-septate; deeply constricted at septa, becoming 3-septate, brown to dark brown when mature, without appendages. **Asexual morph:** Undetermined.

Culture characteristics. Ascospores germinated on PDA within 24 h, and germ tubes produced from basal cell. Colonies growing on PDA reached 17–18 mm in diameter after three weeks at 25 °C in dark, white in the whole colony from above, circular, edge entire, margin well-defined; in reverse, off-white to grayish brown, no pigmentation on PDA.

Material examined. China • Yunnan Province, Xishuangbanna Dai Autonomous Prefecture, Mengla County, Xishuangbanna Tropical Botanical Garden Chinese Academy of Sciences. 21°56'1"N, 101°25'33"E, elevation 505 m, on dead branches of medicinal plant *Citrus medica* L. (Rutaceae), 10 November 2022, H.Z. Du, S655 (HKAS 131311, holotype; HUEST 23.0200, isotype); ex-holotype living culture CGMCC 3.25626; ex-isotype living culture UESTCC 23.0200.

Notes. *Nigrograna longiorostiolata* shares similar morphology with *N. magnoliae* (holotype, MFLU 20–0092) and *N. kunmingensis* (holotype, ZHKU 22-0141) in having immersed, globose to subglobose ascomata, bitunicate and clavate asci, fusoid to ellipsoid, 3-septate mature ascospores. However, the ascomata size of *N. longiorostiolata* (222–293 × 144–486 µm) is larger than *N. magnoliae* (200–300 × 100–150 µm) (Wanasinghe et al. 2020) and smaller than *N. kunmingensis* (300–500 × 390–450 µm) (Liu et al. 2024). The phylogenetic result (Fig. 1) showed that *N. longiorostiolata* (CGMCC 3.25626 and UESTCC 23.0200) can be recognized as a distinct phylogenetic species with high bootstrap support (100% MLBS/1.00 BIPP). Additionally, *N. longiorostiolata* (ex-type strain, CGMCC 3.25626) can be distinguished from *N. magnoliae* (ex-type strain, MFLUCC 20-0020) by 26/471 bp (5.5%, 2 gaps) in ITS, 14/831 bp (1.7%, without gaps) in LSU, 30/855 bp (3.5%, 3 gaps) in *tef1-α* and 96/1042

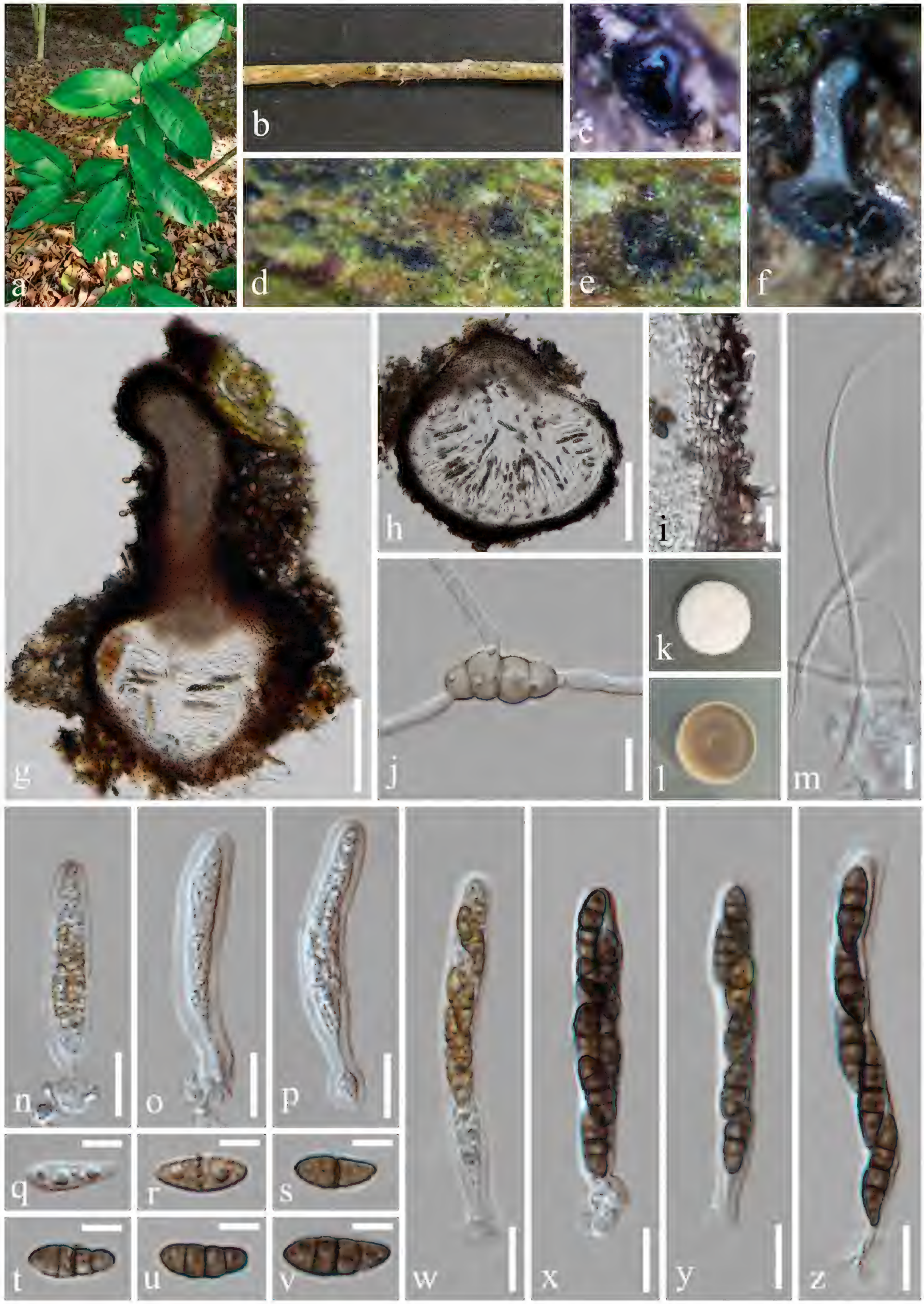

Figure 3. *Nigrograna longiorostiolata* (HKAS 131311, holotype) **a** host *Citrus medica* **b** branch of *Citrus medica* **c–f** appearance of ascomata on host surface **g, h** vertical section through ascoma **i** peridium **j** germinated ascospore **k, l** colony on PDA, above (**k**) and below (**l**) **m** hamathecium **n–p, w–z** asci **q–v** ascospores. Scale bars: 100 µm (**g, h**); 10 µm (**i, j, m–p, w–z**); 5 µm (**q–v**).

bp (9.2%, without gaps) in *rpb2* differences, and differs from *N. kunmingensis* (ex-type strain, ZHKUCC 22-0242) with 70/823 bp (8.5%, 21 gaps) of ITS, 14/844 bp (1.7%, without gaps) of LSU and 30/855 bp (3.5%, 3 gaps) of *tef1-α* differences. Therefore, *N. longiorostiolata* associated with *Citrus medica* is a phylogenetically distinct specie and introduced as a new species.

***Nigrograna acericola* W.L. Li & Jian K. Liu, Mycosphere, 14(1): 1496–1500 (2023)**

MycoBank No: 849155

Fig. 4

Description. ***Saprobic*** on dead branches of *Gymnosporia acuminata* (Celastraceae). **Sexual morph:** ***Ascomata*** 524–647 × 341–475 µm ($\bar{x}$ = 586 × 424 µm, n = 20), solitary, scattered, immersed, ostiolar necks visible on the host surface or erumpent, subglobose to ellipsoid, coriaceous, brown to dark brown, with an ostiole. ***Ostioles*** 86–138 µm long, 64–119 µm wide ($\bar{x}$ = 113 × 96 µm, n = 20), mostly central, some eccentric, with a crest-like apex, central, filled with hyaline periphyses. ***Peridium*** 15–58 µm ($\bar{x}$ = 40 µm, n = 20) µm wide, composed of 4–5 layers of flattened, brown to dark brown, thin-walled cells of ***textura angularis***, the inner layer is dense, the outer layer sparse. ***Hamathecium*** 1.5–3 µm ($\bar{x}$ = 2 µm, n = 20) wide, composed of numerous, filamentous, hyaline, unbranched pseudoparaphyses. ***Asci*** 70–87 × 12–14 µm ($\bar{x}$ = 77 × 13 µm, n = 30), 8-spored, bitunicate, fissitunicate, cylindrical to clavate, short pedicellate, apically rounded, with a minute ocular chamber. ***Ascospores*** 16–19 × 5–7 µm ($\bar{x}$ = 17 × 6 µm, n = 50), 1–2-seriate, biseriate or partially overlapping, fusoid to ellipsoid, with obtuse ends, tapering towards the ends, guttulate, smooth-walled, 1-septate, subhyaline to yellowish-brown when young; becoming 3-septate, slightly constricted at the middle septum, brown to dark brown when mature, without appendages. **Asexual morph:** Undetermined.

Culture characteristics. Ascospores germinated on PDA within 24 h, and germ tubes produced from basal cell. Colonies growing on PDA reached 38–40 mm in diameter after three weeks at 25 °C in dark, white in the whole colony from above, circular, edge entire, margin well-defined; in reverse, light brown in the center, olive gray at the margin, no pigmentation on PDA.

Material examined. China • Yunnan Province, Xishuangbanna Dai Autonomous Prefecture, Mengla County, Xishuangbanna Tropical Botanical Garden Chinese Academy of Sciences. 21°55'54"N, 101°15'16"E, elevation 511 m, on dead branches of medicinal plant *Gymnosporia acuminata* Hook. f. (Celastraceae), 10 November 2022, H.Z. Du, D03 (HUEST 23.0208), living culture UESTCC 23.0208; *ibid*., Sichuan Province, Zigong City, Rong County, 29°29'1"N, 104°14'19"E, elevation 850 m, on dead branches of medicinal plant *Camellia sinensis* (L.) O. Ktze. (Theaceae), 3 November 2022, Y. H. Lu & Y. Xiao, CS11(HUEST 23.0191), living culture UESTCC 23.0191.

Notes. *Nigrograna acericola* was introduced by Li et al. (2023) from *Acer truncatum* (Aceraceae) in China. Our collections are identical to *N. acericola* based on morphology and phylogeny. We reported it as new host records from *Camellia sinensis* and *Gymnosporia acuminata* in China.

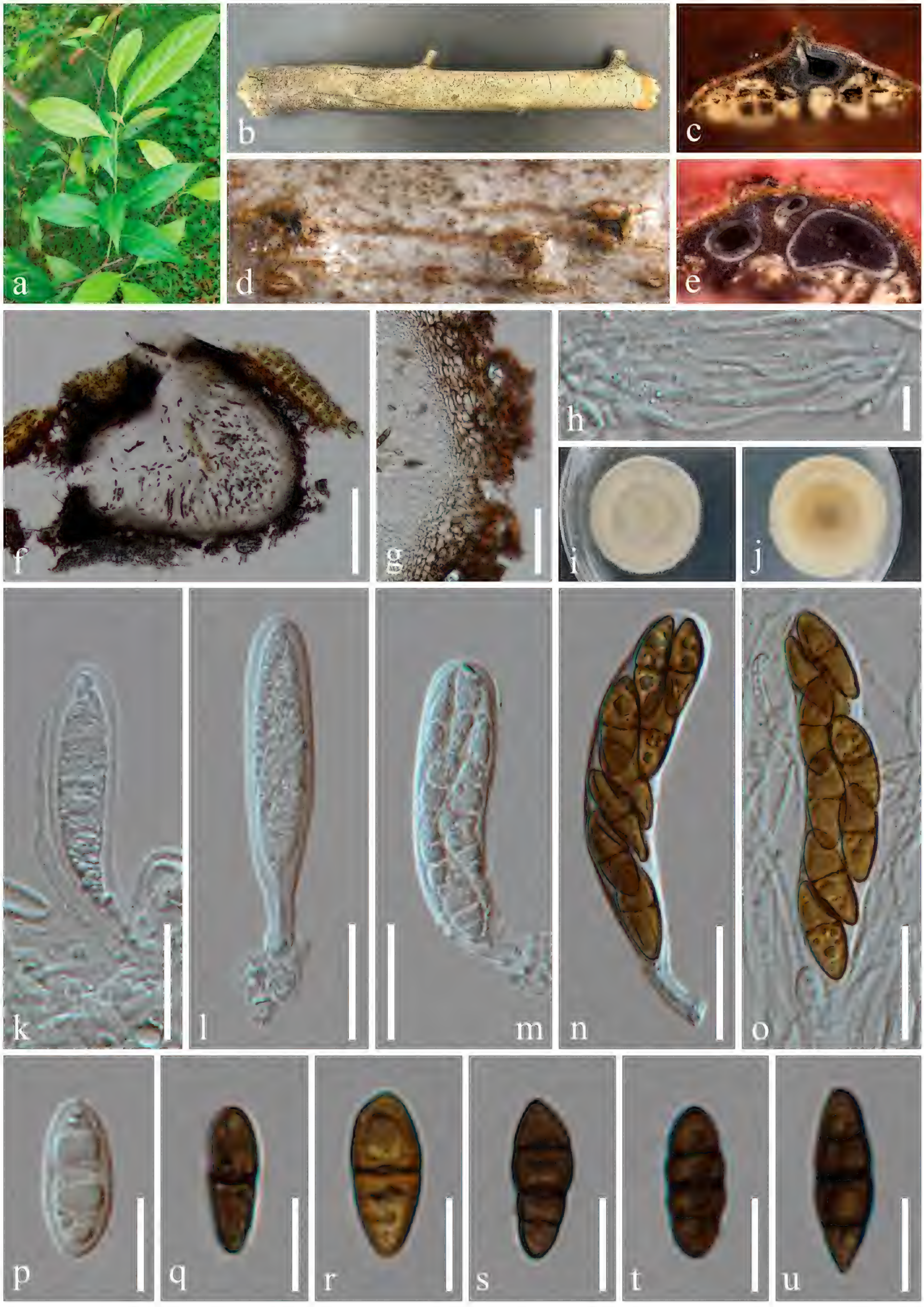

Figure 4. *Nigrograna acericola* (HUEST 23.0208, new host record) **a** host *Gymnosporia acuminata* **b** branch of *Gymnosporia acuminata* **c–e** appearance of ascomata on host surface **f** vertical section through ascoma **g** peridium **h** hamathecium **i, j** colony on PDA, above (**i**) and below (**j**) **k–o** asci. **p–u** ascospores. Scale bars: 200 μm (**f**); 50 μm (**g**); 10 μm (**h, p–u**); 20 μm (**k–o**).

Nigrograna camelliae **Y.H. Lu, H.Z. Du & Jian K. Liu, sp. nov.**
MycoBank No: 854178
Fig. 5

Etymology. The epithet '*camelliae*' refers to the host genus *Camelliae* from which the fungus was originally isolated.

Holotype. HKAS 131310

Description. ***Saprobic*** on dead branches of *Camellia sinensis* (Theaceae). **Sexual morph:** ***Ascomata*** 137–270 µm wide, 208–324 µm high ($\bar{x}$ = 212 × 265 µm, n = 20), solitary, scattered, immersed, black spots on the host substrate, globose to subglobose, sometimes obpyriform, ostiolate, hairs of ascomata 2–3 µm wide, slightly brown, septate. ***Ostioles*** 65–138 µm long, 32–60 µm wide ($\bar{x}$ = 100 × 45 µm, n = 20) mostly central, some eccentric, with a crest-like apex. ***Peridium*** 19–30 µm ($\bar{x}$ = 23 µm, n = 20) wide, composed of 2–3 layers, comprising reddish brown to dark brown pigmented cells. ***Hamathecium*** 2–3 µm ($\bar{x}$ = 2.5 µm, n = 20) wide, composed of numerous, filiform, hyaline, aseptate or separate, filamentous, smooth-walled pseudoparaphyses. ***Asci*** 70–108 × 9–11 µm ($\bar{x}$ = 80 × 10 µm, n = 30), 8-spored, bitunicate, fissitunicate, clavate to cylindric-clavate, short stalked, some with a swollen base, apically rounded, with a small ocular chamber. ***Ascospores*** 13–16 × 4–6 µm ($\bar{x}$ = 15 × 5 µm, n = 50), overlapping uni- to bi-seriately arranged, fusoid to ellipsoid, tapering towards the blunt ends, or blunt at both ends, straight or slightly curved, 1-septate, constricted, with obviously guttulate, hyaline to slightly brown when immature, pale brown to brown when mature, without appendages. **Asexual morph:** Undetermined.

Culture characteristics. Ascospores germinated on PDA within 24 h, and germ tubes produced from basal cell. Colonies growing on PDA reached 35–36 mm in diameter after three weeks at 25 °C in dark, white in the whole colony and slightly bright yellow in the center from above, circular, edge entire, margin well-defined; in reverse, yellowish brown in the center, slightly brown at the margin and presented an outer ring, no pigmentation on PDA.

Material examined. CHINA • Sichuan Province, Yaan City, Mingshan County, Mengding Mountain. 30°4'32"N, 103°2'23"E, elevation 1,200 m, on dead branches of medicinal plant *Camellia sinensis* (L.) O. Ktze. (Theaceae), 16 July 2023, Y. H. Lu & X. D. Liang, MD03A (HKAS 131310, holotype; HUEST 23.0197, isotype); ex-holotype living culture CGMCC 3.25625; ex-isotype living culture UESTCC 23.0197.

Notes. *Nigrograna camelliae* is phylogenetically close to *N. coffeae* and represents as a distinct lineage (Fig. 1). Additionally, the nucleotide base pair comparison between *N. camelliae* (ex-type strain, CGMCC 3.25625) and *N. coffeae* (ex-type strain, ZHKUCC 22-0210) revealed 15/514 bp (2.9%, 1 gap) of ITS, 11/698 bp (1.6%, without gaps) of LSU, 74/739 bp (10.0% without gaps) of *rpb2* and 28/914 bp (3.1%, without gaps) of *tef1-α* differences. Furthermore, *N. camelliae* morphologically resembles *N. coffeae* in having immersed ascomata, clavate and short pedicellate asci, pale brown to brown and septate ascospores with obviously guttulate (Lu et al. 2022). However, *N. camelliae* differs from *N. coffeae* in having ascomata with hairs and ostioles, solitary or scattered in the substrate. Additionally, they can be distinguished in having larger ascomata (208–324 × 137–270 µm vs. 140–200 × 90–140 µm) and asci (70–108 × 9–11 µm vs. 50–70 × 7–11 µm). Therefore, *N. camelliae* is introduced as a new species with the justification of phylogenetic and morphological evidence.

Figure 5. *Nigrograna camelliae* (HKAS 131310, holotype) **a** host *Camellia sinensis* **b** branch of *Camellia sinensis* **c–e** appearance of ascomata on host surface **f, g** vertical section through ascoma **h** peridium **i** hairs on ascomata **j–m, w, x** asci **n–s** ascospores **t** germinated ascospore **u, v** colony on PDA, above (**u**) and below (**v**). Scale bars: 100 µm (**f, g**); 20 µm (**h–m, w, x**); 5 µm (**n–s**); 10 µm (**t**).

***Nigrograna oleae* W.L. Li & Jian K. Liu, Mycosphere, 14(1): 1503–1505 (2023)**
MycoBank No: 849157
Fig. 6

= *Nigrograna trachycarpi*, MycoKeys 100: 141 (2023).

Description. ***Saprobic*** on dead branches of *Ardisia crenata* (Primulaceae). **Sexual morph:** ***Ascomata*** 190–334 µm wide, 303–406 µm high ($\bar{x}$ = 233 × 370 µm, n = 20), solitary or gregarious, scattered, immersed, often lying parallelly or obliquely to the bark or host surface, with a cylindrical ostiolar neck, coriaceous, obpyriform, brown to dark brown. ***Ostioles*** central or eccentric, filled with hyaline periphyses. ***Peridium*** 16.5–25 µm ($\bar{x}$ = 21 µm, n = 20) wide, consisting 4–6 layers of brown-walled cells of ***textura angularis***. ***Hamathecium*** 1–2 µm ($\bar{x}$ = 1.5 µm, n = 20) wide, aseptate or separate, composed of numerous, filiform, smooth-walled pseudoparaphyses. ***Asci*** 62–127 × 9–12 µm ($\bar{x}$ = 82 × 10 µm, n = 30), 8-spored, bitunicate, fissitunicate, clavate to long cylindric-clavate, with a short pedicel, apically rounded, with a smaller ocular chamber. ***Ascospores*** 14–17 × 4–6 µm ($\bar{x}$ = 15 × 5 µm, n = 50), 1–2-seriate, fusoid to ellipsoid, apical cell mostly obtuse, straight or slightly curved, guttulate, smooth-walled, 3-septate, constricted at the septa, pale brown to yellow-brown when young, brown to chocolate-brown at maturation, without appendages. **Asexual morph:** Undetermined.

Culture characteristics. Ascospores germinated on PDA within 24 h, and germ tubes produced from basal cell. Colonies growing on PDA reached 22–23 mm in diameter after three weeks at 25 °C in dark. Colonies from above, circular, margin entire, dense, surface smooth, velvety appearance, white in the center, presented a pale greenish furrowed ring, white to cream at the margin; in reverse, brown in the central point, brown-gray in the middle, white to pale brownish at the edge, no pigmentation on PDA.

Material examined. China • Yunnan Province, Xishuangbanna Dai Autonomous Prefecture, Mengla County, Xishuangbanna Tropical Botanical Garden Chinese Academy of Sciences. 21°55'49"N, 101°15'19"E, elevation 516 m, on dead branches of medicinal plant *Ardisia crenata* Sims (Primulaceae), 10 November 2022, H.Z. Du, D01 (HUEST 23.0209), living culture UESTCC 23.0209; • ibid., Sichuan Province, Chengdu City, Pujiang County, 30°11'42"N, 103°22'21"E, elevation 630 m, on dead branches of *Camellia sinensis* (L.) O. Ktze. (Theaceae), 5 October 2022, Y.H. Lu & Y. Xiao, A11 (HUEST 23.0193), living culture UESTCC 23.0193.

Notes. *Nigrograna oleae* was introduced by Li et al. (2023) from *Olea europaea* and *N. trachycarpi* was described by Hu et al. (2023) from *Trachycarpus* sp. in China. In this study, multi-locus phylogeny indicated that our two isolates clustered together with *N. oleae* (ex-type strain, CGMCC 3.24423) and *N. trachycarpi* (ex-type strain, GMB0499) by strong support (100% MLBS/1.00 BIPP) (Fig. 1). In addition, the nucleotide base pair comparison of ex-type strain between *N. oleae* (CGMCC 3.24423) and *N. trachycarpi* (GMB0499) was identical by 421/421 bp (100%) of ITS, and 466/466 bp (100%) of *tef1-α*. Additionally, our newly collected specimens share similar morphology with *N. oleae* and *N. trachycarpi*. Therefore, we identify our collections as *N. oleae* and propose the synonymy of *N. trachycarpi* under *N. oleae* based on morphology and phylogeny. The new host records for *N. oleae* from medicinal plants *Ardisia crenata* and *Camellia sinensis* are reported in this study.

Figure 6. *Nigrograna oleae* (HUEST 23.0209, new host record) **a** host *Ardisia crenata* **b** branch of *Ardisia crenata* **c–f** appearance of ascomata on host surface **g, h** vertical section through ascoma **i** peridium **j–l** asci **m–q** ascospores **r, s** colony on PDA, above (**r**) and below (**s**). Scale bars: 100 μm (**g, h**); 20 μm (**i–l**); 10 μm (**m–q**).

Nigrograna thymi **Mapook, Camporesi & K.D. Hyde, Fungal Diversity, 87: 68–70 (2017)**

MycoBank No: 552958

Fig. 7

Description. ***Saprobic*** on dead branches of *Huangtcia renifolia* (Fabaceae). **Sexual morph:** ***Ascomata*** 292–359 µm wide, 166–278 µm high ($\bar{x}$ = 327 × 218 µm, n = 20), solitary or scattered, immersed or semi-immersed to slightly erumpent through host tissue, coriaceous, globose to subglobose, brown to dark brown, hairs of ascomata 2–3 µm wide, brown, septate, branched. ***Ostiole*** inconspicuous, without papillate. ***Peridium*** 15–44 µm ($\bar{x}$ = 29.5 µm, n = 20) wide, 5–6 layers, comprising dark brown cells of ***textura angularis***. ***Hamathecium*** comprising 1–3 µm ($\bar{x}$ = 2 µm, n = 20) wide, cylindrical to filiform, septate, branched, smooth-walled pseudoparaphyses. ***Asci*** 43–86 × 7–9 µm ($\bar{x}$ = 66 × 8 µm, n = 30), 8-spored, bitunicate, cylindrical to broadly filiform, with small ocular chamber. ***Ascospores*** 11–15 × 4–6 µm ($\bar{x}$ = 13 × 4.5 µm, n = 50), 1–2-seriate, overlapping, broadly fusiform to inequilateral, widest at the middle cell, guttulate, smooth-walled, aseptate or 1-septate, hyaline when immature, becoming 3-septate, slightly constricted at the septum, pale brown to brown at maturity, without appendages. **Asexual morph:** Undetermined.

Culture characteristics. Ascospores germinated on PDA within 24 h, and germ tubes produced from basal cell. Colonies growing on PDA reached 20 mm in diameter after three weeks at 25 °C in dark. Colonies from above, white in the whole colony and raised in the center, circular, edge entire, margin well-defined; in reverse, grayish-green in the center, white to pale green ring at the margin, no pigmentation on PDA.

Material examined. CHINA • Yunnan Province, Xishuangbanna Dai Autonomous Prefecture, Mengla County, Xishuangbanna Tropical Botanical Garden Chinese Academy of Sciences. 21°55'50"N, 101°15'29"E, elevation 515 m, on dead branches of medicinal plant *Huangtcia renifolia* (L.) H. Ohashi & K. Ohashi (Fabaceae), 10 November 2022, H.Z. Du, D02 (HUEST 23.0210), living culture UESTCC 23.0210; • ibid., Sichuan Province, Leshan City, Emeishan County, 29°36'10"N, 103°21'54"E, elevation 1,100 m, on dead branches of *Camellia sinensis* (L.) O. Ktze. (Theaceae), 18 July 2023, Y.H. Lu & X.D. Liang, EM03 (HUEST 23.0194), living culture UESTCC 23.0194.

Notes. *Nigrograna thymi* was introduced by Hyde et al. (2017) from *Thymus oenipontanus* in Italy. Our collections are identical to *N. thymi* based on morphology and phylogeny (Fig. 1). We reported it as new host records from medicinal plants *Huangtcia renifolia* and *Camellia sinensis* in China.

Nigrograna neriicola **Y.H. Lu, H.Z. Du & Jian K. Liu, sp. nov.**

MycoBank No: 854179

Fig. 8

Etymology. The epithet '*neriicola*' refers to the host genus *Nerium* from which the fungus was originally isolated.

Holotype. HKAS 131313.

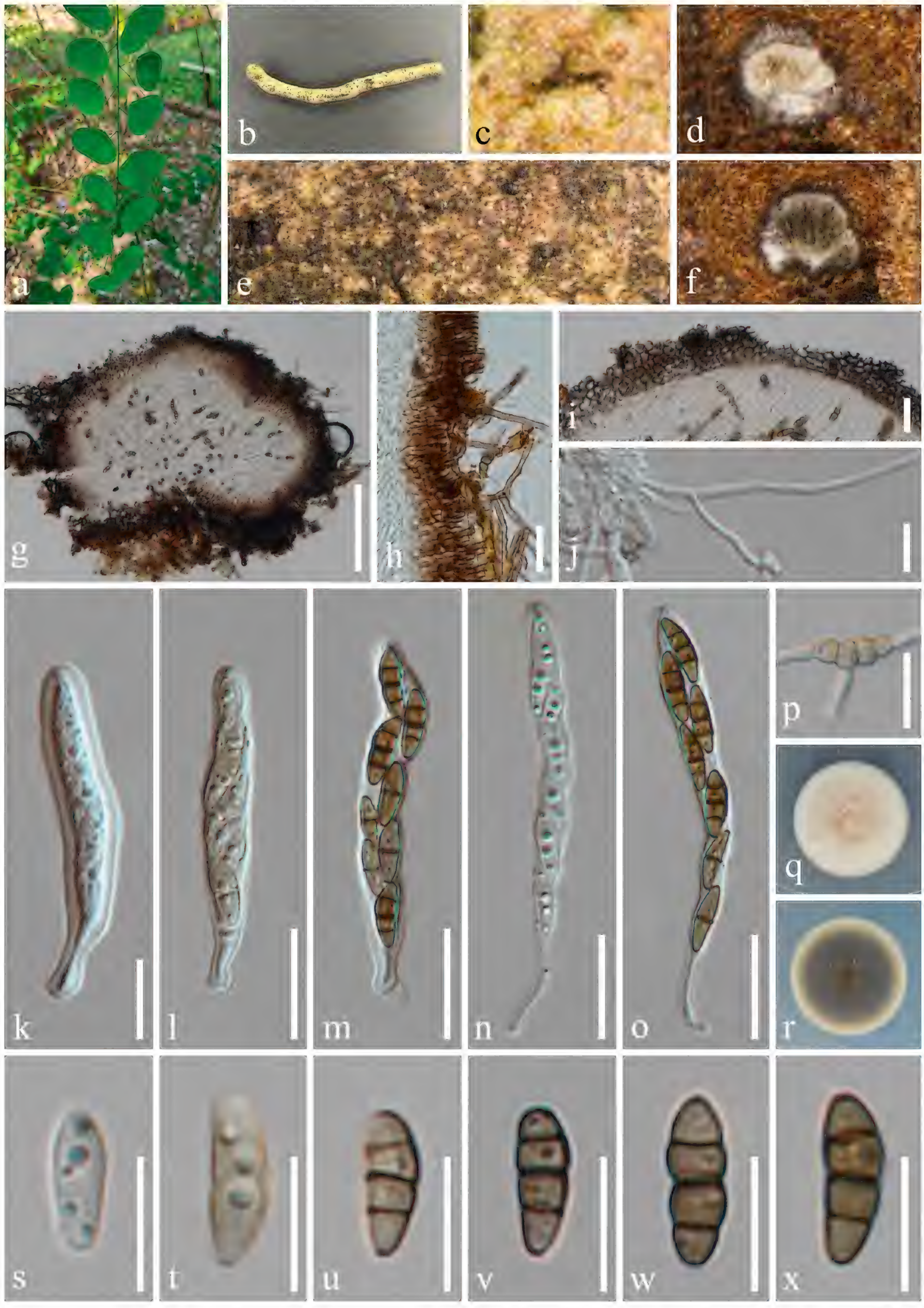

Figure 7. *Nigrograna thymi* (HUEST 23.0210, new host record) **a** host *Huangtcia renifolia* **b** branch of *Huangtcia renifolia* **c–f** appearance of ascomata on host surface **g** vertical section through ascoma **h** hairs on ascomata **i** peridium **j** hamathecium **k–o** asci **p** germinated ascospore **q, r** colony on PDA, above (**q**) and below (**r**) **s–x** ascospores. Scale bars: 100 µm (**g**); 20 µm (**h, i, l–p**); 10 µm (**j, k, s–x**).

Description. ***Saprobic*** on dead branches of *Nerium oleander* (Apocynaceae). **Sexual morph:** ***Ascomata*** 138–231 µm wide, 156–251 µm high ($\bar{x}$ = 182 × 202 µm, n = 20), mostly gregarious, sometimes solitary, scattered, immersed to semi-immersed, appearing as black irregular protrusions and cracks, globose to subglobose, sometimes obpyriform, dark brown to black, with an ostiole. ***Ostioles*** 32–54 µm long, 14–34 µm wide ($\bar{x}$ = 45 × 25 µm, n = 20) mostly central, some eccentric, with a crest-like apex. ***Peridium*** 16–61 µm ($\bar{x}$ = 32 µm, n = 20) wide, multi-layered, reticulate structure, comprising dark brown to reddish brown pigmented cells of ***textura angularis***. ***Hamathecium*** 1–2.5 µm wide ($\bar{x}$ = 2 µm, n = 20), composed of numerous, filiform, hyaline, aseptate or separate, rarely branched, filamentous, smooth-walled pseudoparaphyses. ***Asci*** 35–80 × 7–10 µm ($\bar{x}$ = 56 × 8.5 µm, n = 30), 8-spored, bitunicate, fissitunicate, clavate to cylindric-clavate, short stalked, some with club-shape pedicel, apically rounded with a small ocular chamber. ***Ascospores*** 12–21(–31) × 3.5–5 µm ($\bar{x}$ = 16 × 4 µm, n = 50), uni- to bi-seriately arranged, partially overlapping, fusoid to ellipsoid, tapering towards the blunt ends, or blunt at both ends, straight or slightly curved, guttulate, smooth-walled, 1-septate, subhyaline to slightly brown when young; becoming 3-septate, yellowish-brown to dark brown when mature, deeply constricted at septa, without appendages. **Asexual morph:** Undetermined.

Culture characteristics. Ascospores germinated on PDA within 24 h, and germ tubes produced from basal cell. Colonies growing on PDA reached 33–35 mm in diameter after one month at 25 °C in dark, slightly brown in the whole colony and raised in the central point from above, circular, edge entire, margin well-defined, aerial mycelia dense; in reverse, black-brown in the center, slightly brown ring at the margin, no pigmentation on PDA.

Material examined. CHINA • Yunnan Province, Xishuangbanna Dai Autonomous Prefecture, Mengla County, Xishuangbanna Tropical Botanical Garden Chinese Academy of Sciences. 21°55'52"N, 101°15'29"E, elevation 505 m, on dead branches of medicinal plant *Nerium oleander* L. (Apocynaceae), 10 November 2022, H.Z. Du, D04 (HKAS 131313, holotype); ex-holotype living culture CGMCC 3.25624; • ibid., Sichuan Province, Chengdu City, Pujiang County. 30°11'40"N, 103°22'25"E, elevation 600 m, on dead branches of *Camellia sinensis* (L.) O. Ktze. (Theaceae), 5 October 2022, Y.H. Lu & Y. Xiao, M03 (HUEST 23.0195, paratype); ex-paratype living culture UESTCC 23.0195.

Notes. *Nigrograna neriicola* (CGMCC 3.25624 and UESTCC 23.0195) has close phylogenetic relationships with *N. schinifolii* (GMB0498 and GMB0504) but formed a distinct lineage (Fig. 1). Morphologically, the ascomata of *N. neriicola* differs from *N. schinifolii* in having black irregular protrusions and cracks, mostly gregarious, and ascospores that are slightly larger than *N. schinifolii* (12–21 × 3.5–5 µm vs. 10–14 × 2.8–4 µm) (Hu et al. 2023). Additionally, the nucleotide base pair comparison between *N. neriicola* (ex-type strain, CGMCC 3.25624) and *N. schinifolii* (ex-type strain, GMB0498) revealed no significant differences by 375/377 bp (99.5%, 1 gap) of ITS and 507/511 bp (99.2%, without gaps) of *tef1-α*. However, for *tef1-α* gene, the length of the two *N. schinifolii* strains (GMB0498 and GMB0504) is only 511 bp. The problem of low similarity occurred after the blastn search without a corresponding sequence in the same genus for alignment. Therefore, *N. neriicola* is introduced as a new species with the morpho-molecular data analysis.

Figure 8. *Nigrograna neriicola* (HKAS 131313, holotype) **a** host *Nerium oleander* **b** branch of *Nerium oleander* **c–f** appearance of ascomata on host surface **g, h** vertical section through ascoma **i** peridium **j–n** asci **o–v** ascospores **w** germinated ascospore **x** hamathecium **y, z** colony on PDA, above (**y**) and below (**z**). Scale bars: 200 µm (**g, h**); 100 µm (**i**); 20 µm (**j–n, x**); 5 µm (**o–v**); 10 µm (**w**).

Nigrograna guttulata **Y.H. Lu, H.Z. Du & Jian K. Liu, sp. nov.**
MycoBank No: 854180
Fig. 9

Etymology. The epithet '*guttulata*' refers to the guttulate ascospores.

Holotype. HKAS 131992.

Description. ***Saprobic*** on dead branches of *Camellia sinensis* (Theaceae). **Sexual morph:** ***Ascomata*** 182–283 µm wide, 106–276 µm high ($\bar{x}$ = 241 × 183 µm, n = 20), solitary, immersed, ostiolar necks visible on the host surface or erumpent, triangular, globose to subglobose, sometimes obpyriform, coriaceous, ostiolate, dark brown to black. ***Ostioles*** 35–61 µm long, 15–30 µm wide ($\bar{x}$ = 47 × 22 µm, n = 20) mostly central, some eccentric, filled with hyaline periphyses. ***Peridium*** 15–37 µm ($\bar{x}$ = 25 µm, n = 20) wide, multi-layered, reticulate structure, comprising dark brown to reddish brown pigmented cells of ***textura angularis***. ***Hamathecium*** 1–2.5 µm wide ($\bar{x}$ = 2 µm, n = 20), composed of numerous, filiform, hyaline, aseptate or separate, some branched, filamentous, smooth-walled pseudoparaphyses. ***Asci*** 35–70 × 7–12 µm ($\bar{x}$ = 48 × 8.5 µm, n = 30), 8-spored, bitunicate, fissitunicate, clavate to cylindric-clavate, short stalked, some with club-shape pedicel, apically rounded, with small ocular chamber. ***Ascospores*** 10–13 × 3–5 µm ($\bar{x}$ = 12 × 4 µm, n = 50), 1–2-seriate, overlapping, fusoid to ellipsoid, tapering towards the blunt ends, or blunt at both ends, straight or slightly curved, guttulate, smooth-walled, subhyaline to slightly brown when young, 1-septate; yellowish-brown to dark brown when mature, becoming 3-septate, deeply constricted at septa, without appendages. **Asexual morph:** Undetermined.

Culture characteristics. Ascospores germinated on PDA within 24 h, and germ tubes produced from basal cell. Colonies growing on PDA reached 35–38 mm in diameter after one month at 25 °C in dark. Colonies from above, white in the whole colony and raised in the central point, circular, margin well-defined, aerial mycelia dense; in reverse, grayish green in the center, white ring at the margin, no pigmentation on PDA.

Material examined. China • Guizhou Province, Guiyang City, Huaxi District, 26°30'40"N, 106°39'30"E, elevation 1,155 m, on dead branches of medicinal plant *Camellia sinensis* (Linnaeus) Kuntze (Theaceae), 2 February 2023, Y.X. Yu & Y.H. Lu, GY15 (HKAS 131992, holotype; HUEST 23.0295, isotype), ex-holotype living culture CGMCC 3.25689; ex-isotype living culture UESTCC 23.0295.

Notes. *Nigrograna peruviensis* was reported by Kolařík et al. (2017) as an endophytic fungus (*Biatriospora peruviensis*) and was synonymized under the genus *Nigrograna* by Kolařík (2018), but with a lack of detailed morphological structures. In this study, our isolates of *N. guttulata* (CGMCC 3.25689 and UESTCC 23.0295) have a close phylogenetic relationship with *N. peruviensis* (Kolařík et al. 2017; Kolařík 2018) based on ITS, LSU, *rpb2*, SSU, and *tef1-α* sequence data, and formed a distinct lineage with absolute bootstrap support (100% MLBS/1.00 BIPP) (Fig. 1). Additionally, *N. guttulata* (ex-type strain, CGMCC 3.25689) can be distinguished from *N. peruviensis* (ex-type strain, CCF 4485) by 8/462 bp (1.7%, 3 gaps) in ITS, 24/1020 bp (2.4%, without gaps) in LSU and 10/618 bp (1.6%, without gaps) in *rpb2* differences. Therefore, the establishment of the new species *N. guttulata* is justified by the phylogenetic evidence.

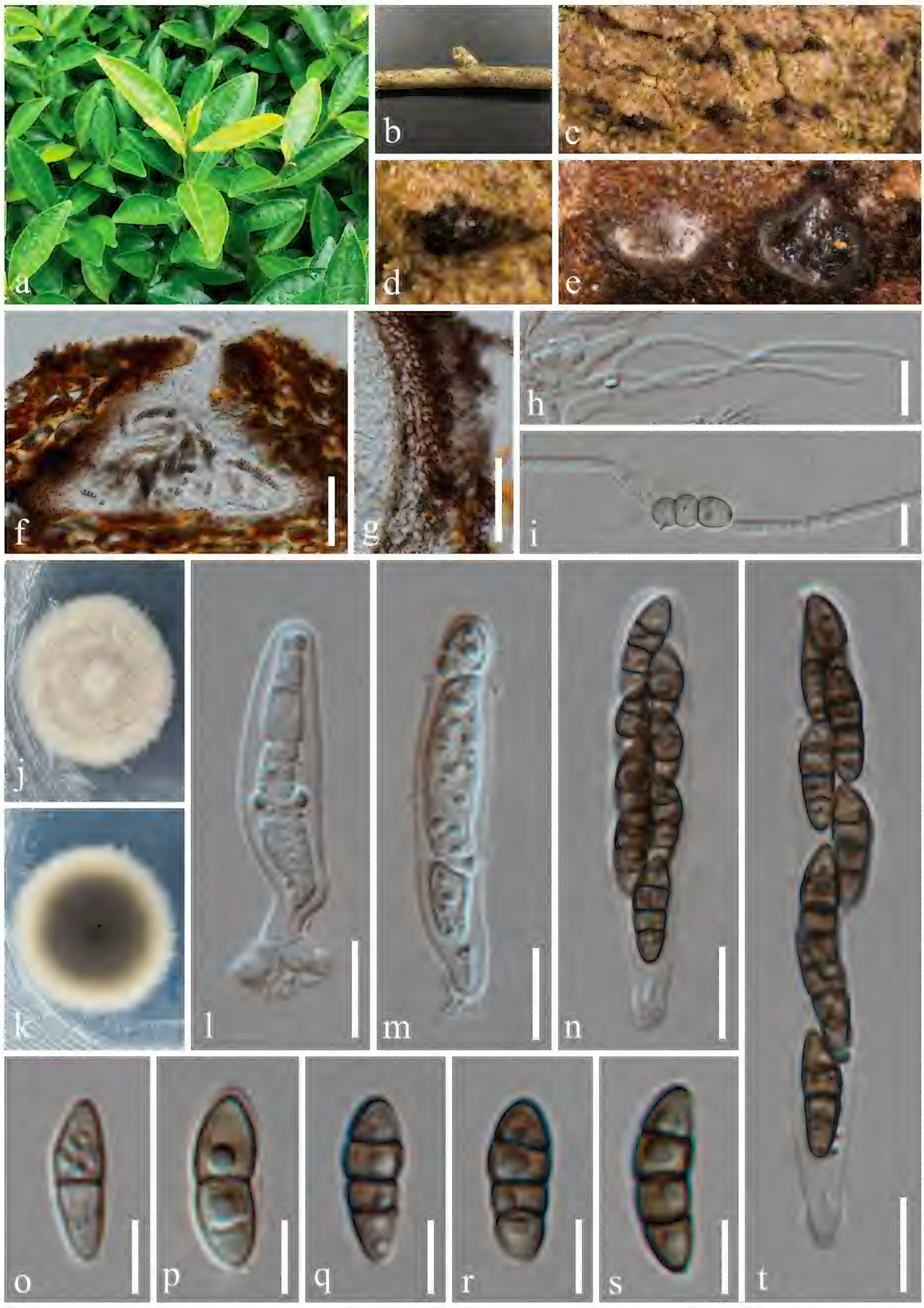

Figure 9. *Nigrograna guttulata* (HKAS 131992, holotype) **a** host *Camellia sinensis* **b** branch of *Camellia sinensis* **c–e** appearance of ascomata on host surface **f** vertical section through ascoma **g** peridium **h** hamathecium **i** germinated ascospore **j, k** colony on PDA, above (**j**) and below (**k**) **l–n, t** asci **o–s** ascospores. Scale bars: 50 µm (**f**); 40 µm (**g**); 10 µm (**h, i, l–n, t**); 5 µm (**o–s**).

Discussion

In this study, eighteen isolates of *Nigrograna* (Nigrograna ceae, Pleosporales, Dothideomycetes) were obtained from medicinal plants in Southwest China (Guizhou, Sichuan and Yunnan Provinces). Based on morphological and culture characteristics, and phylogenetic analyses of combined ITS, LSU, *rpb2*, SSU, and *tef1-α* sequence data, four novel species were identified, namely *Nigrograna camelliae*, *N. guttulata*, *N. longiorostiolata* and *N. neriicola*, Additionally, our known species, namely *N. acericola*, *N. magnoliae*, *N. oleae* and *N. thymi*, were reported from medical plants as new host records. These isolates were associated with terrestrial habitat and collected from medicinal plants in nine plant families, including Apocynaceae, Berberidaceae, Buxaceae, Celastraceae, Eucommiaceae, Fabaceae, Primulaceae, Rutaceae, and Theaceae.

Species within the genus *Nigrograna* exhibit considerable morphological similarity, often complicating species delimitation based solely on morphological traits (Jaklitsch and Voglmayr 2016; Zhang et al. 2020; Lu et al. 2022; Li et al. 2023). As such, molecular data play a critical role in species identification. For example, Jaklitsch and Voglmayr (2016) demonstrated that morphologically similar species, such as *N. coffeae* and *N. camelliae*, can be distinguished phylogenetically. These species sequence divergence across multiple loci, including (15/514 bp, 2.9%, 1 gap), LSU (11/698 bp, 1.6%, without gaps), *rpb2* (74/739 bp, 10.0%, without gaps) and *tef1-α* (28/914 bp, 3.1%, without gaps), highlighting the importance of molecular analysis for accurate taxonomic placement. *Nigrograna* is a worldwide distributed genus, with species reported from Asia (Dayarathne et al. 2020; Mapook et al. 2020; Zhang et al. 2020; Lu et al. 2022; Li et al. 2023), the Americas, and Europe (Jaklitsch and Voglmayr 2016; Hyde et al. 2017; Kolařík et al. 2017; Tibpromma et al. 2017; Kolařík 2018; Zhao et al. 2018; Dayarathne et al. 2020; Wanasinghe et al. 2020). While certain species, such as *N. carollii*, *N. peruviensis* and *N. yasuniana*, have been reported as endophytes on various hosts (Kolařík et al. 2017), the majority of known species are saprotrophs on the bark or corticated twigs and branches of various hardwoods (Jaklitsch and Voglmayr 2016; Mapook et al. 2020; Zhang et al. 2020; Lu et al. 2022; Hu et al. 2023; Li et al. 2023). Reports of *Nigrograna* species on flowers, fruits, leaves, or herbaceous plants are rare, indicating a preference for woody hosts. Consistent with these findings, the isolates in this study were primarily recovered from the branches of medicinal woody plants, such as *Eucommia ulmoides* (Eucommiaceae), *Gymnosporia acuminata* (Celastraceae), and *Mahonia bealei* (Berberidaceae).

It is noteworthy that *Nigrograna magnoliae* was isolated from the bark of *Eucommia ulmoides*, which is a primary medicinal component of the plant. The quality of medicinal plants is closely tied to their clinical efficacy, and the presence of fungal species such as *N. magnoliae* raises important questions about the potential impact of fungal colonization on the medicinal properties of their hosts (Balekundri and Mannur 2020; Rasool et al. 2020; Ali et al. 2021). This finding warrants further investigation to assess whether *N. magnoliae* could affect the quality or bioactive compounds of *E. ulmoides*. In addition to their ecological diversity, certain species within *Nigrograna* have been found to produce bioactive secondary metabolites. For instance, *Nigrograna rubescens* has been reported to produce naphthoquinone compounds, which are known for their broad spectrum

of biological activities (Naysmith et al. 2017; Mack et al. 2024). These metabolites share structural similarities with those found in *N. antibiotica*, which also produces bioactive compounds (Stodůlková et al. 2014). Such findings suggest that members of *Nigrograna* have significant potential for biotechnological applications, particularly in drug discovery. Understanding the relationships between *Nigrograna* species and their medicinal plant hosts, as well as the impact of fungal colonization on the quality of these plants, remains a critical area of research.

In conclusion, this study highlights the diversity of *Nigrograna* species associated with medicinal plants in Southwest China and underscores the importance of integrating morphological and molecular data for accurate species identification. Given the potential ecological and economic implications of *Nigrograna* colonization on medicinal plants, continued research is essential. Detailed taxonomic and ecological studies of *Nigrograna* from medicinal plants will provide valuable insights into the species diversity, host specificity, and potential biotechnological applications of this genus. Ongoing efforts to collect and analyze fresh isolates will further enhance our understanding of the genus and its broader ecological and medicinal significance.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: HZD, JKL. Data curation: HZD, YHL, RC. Formal analysis: HZD, YHL, JKL. Funding acquisition: JKL. Investigation: HZD, YHL. Methodology: HZD. Project administration: HZD, JKL, RC. Supervision: JKL, RC. Writing – original draft: HZD. Writing – review & editing: HZD, JKL. All authors have read and agreed to the published version of the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text.

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